

***Lacantunia enigmatica* (Teleostei: Siluriformes) a new and phylogenetically puzzling freshwater fish from Mesoamerica**

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Abstract

A new family (Lacantuniidae), genus and species of catfish, *Lacantunia enigmatica*, is described from the Río Usumacinta basin of Chiapas, México. This odd siluriform is diagnosed by five distinctively autapomorphic and anatomically complex structures. The fifth (last) infraorbital bone is relatively large, anteriorly convex and remote from a prominent sphenotic process. The lateral margin of the frontal, lateral ethmoid and sphenotic bones are thick at the origins of much enlarged adductor mandibulae and levator arcus palatini muscles; otherwise the skull roof is constricted and flat. One pair of cone-shaped "pseudo-pharyngobranchial" bones is present at the anterior tips of enlarged cartilages medial to the first epibranchial. A hypertrophied, axe-shaped uncinat process emerges dorsally from the third epibranchial. The gas bladder has paired spherical, unencapsulated diverticulae protruding from its anterodorsal wall. *Lacantunia enigmatica* cannot be placed within or as a basal sister lineage to any known catfish family or multifamily clade except Siluroidei. This species may represent an ancient group, perhaps of early Tertiary age or older, and it adds another biogeographic puzzle to the historically complex Mesoamerican biota.

Key words: Siluriformes, catfishes, México, Río Usumacinta, taxonomy, phylogeny, biogeography

Resumen

Se describe una nueva familia (Lacantuniidae), género y especie de bagre, *Lacantunia enigmatica*, proveniente de la cuenca del río Usumacinta, Chiapas, México. Cinco estructuras autapomórficas y anatómicamente complejas diagnostican a este especial siluriforme. El quinto (último) hueso

infraorbital es relativamente largo, convexo anteriormente y remoto de un proceso esfenótico prominente. Los márgenes laterales del frontal, del etmoide lateral y del esfenótico son gruesos en los orígenes de los músculos adductor mandibulae y levator arcus palatini y la bóveda craneana es plana y estrecha. Un par de huesos “pseudofaringobranquiales” en forma de cono se encuentra en los extremos anteriores de cartílagos mediales agrandados del primer epibranquial. Del tercer epibranquial surge dorsalmente un proceso uncinado hipertrofiado en forma de hacha. La vejiga natatoria tiene un par de divertículos esféricos prominentes no encapsulados que surgen de la pared anterodorsal. *Lacantunia enigmatica* no puede ser ubicada dentro o como un descendiente basal hermano de ninguna familia o clado multifamiliar conocido excepto Siluroidei. Esta especie podría representar un grupo ancestral quizás del Terciario temprano o más antiguo y se agrega otra interrogante biogeográfica a la biota Mesoamericana históricamente compleja.

Palabras clave: Siluriformes, bagres, México, río Usumacinta, taxonomía, filogenia, biogeografía

Introduction

While discoveries of new fish species continue at a high rate, new finds of deep phylogenetic lines of any living vertebrates are rare (Lundberg *et al.* 2000). So it is for catfishes, Siluriformes, a globally diverse clade of mostly freshwater fishes with nearly 3,000 known living species plus an estimated 1,750 undescribed species (Eschmeyer 1998, All Catfish Species Inventory Project 2004). Over the last six years the annual average number of published descriptions of new catfish species has come to approach 50, more than doubling earlier publication rates (Eschmeyer 1998, All Catfish Species Inventory Project 2004). Most newly found catfishes are small (less than 20 cm standard length, SL), from poorly explored tropical waters, and belong to established, often recently revised, genera. The catfish reported here as *Lacantunia enigmatica* n. fam., n. gen. and n. sp. (Figs. 1, 2) is a striking exception. *Lacantunia* lives in southern México's Río Usumacinta (Rosen 1979, Rodiles-Hernández in press), a relatively well explored river system. This species approaches 0.5 m SL and is commonly fished by local people who call it "*madre de juil*" (meaning "mother of *Rhamdia*," another local catfish). Yet, ichthyologists missed this conspicuous fish until 1996 when one of us (RRH) collected the first specimens for study in tributaries near the Chiapas-Guatemalan border (Fig. 3). Although *Lacantunia* bears a superficial resemblance to North American Ictaluridae, our phylogenetic evaluation shows that the species is neither an ictalurid nor a member of any of the other 35 catfish families. Given its unresolved and apparently deep systematic position and provenance in one of the world's most historically complex biotas (Savage 1982, Miller *et al.* in press), *Lacantunia* is a phylogenetic and biogeographic enigma. Here we describe this new catfish and report the findings of our first assessment of its phylogenetic position among living and fossil siluriforms. Our continuing investigation of the relationships of *Lacantunia* using morphological and molecular data sets will be published elsewhere.

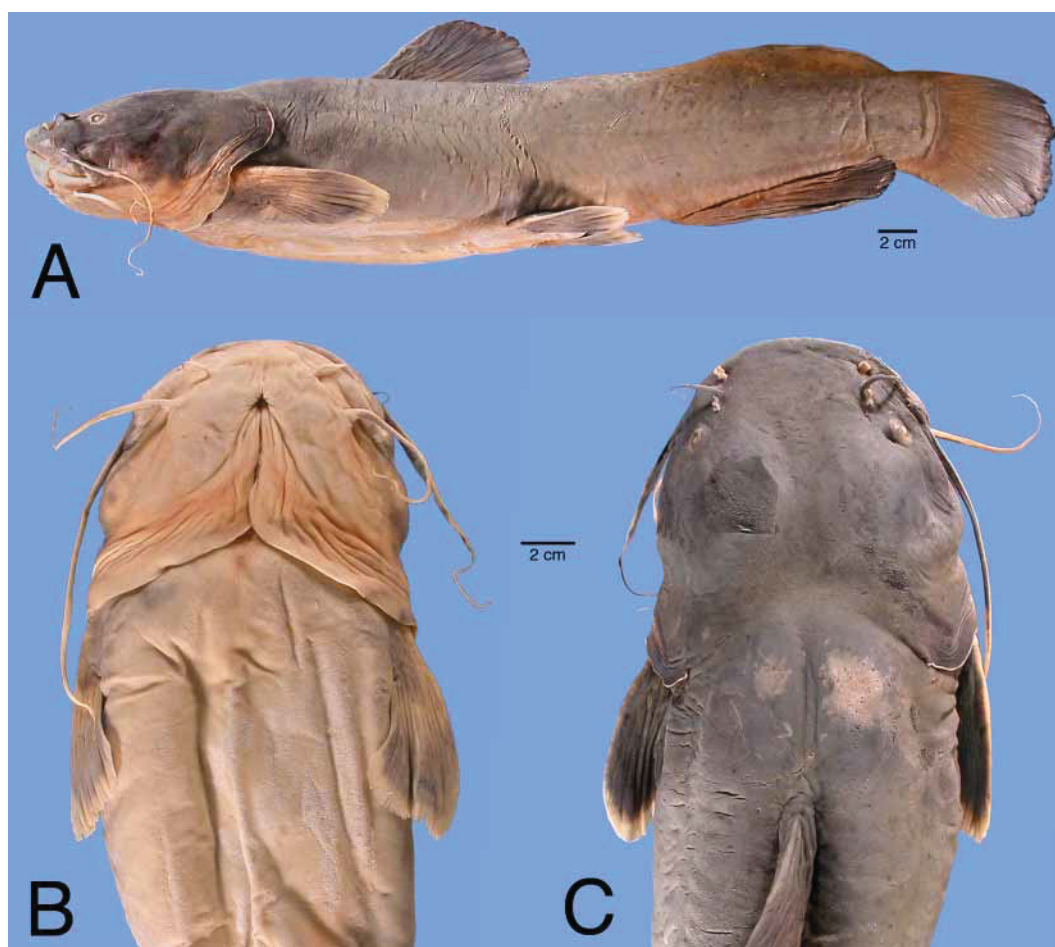


FIGURE 1. *Lacantunia enigmatica*, Holotype specimen ECO-SC 3859, 427 mm SL. A. Lateral view. B. Ventral view. C. Dorsal view.

Material and Methods

The specimens described herein were collected by angling and gill nets at night in the fast flowing, steep gradient and rocky stretches and deep pools of the Río Lacantún and Río Lacanjá.

Osteological characters were examined in articulated and disarticulated dry skeletal preparations, and in High Resolution X-ray Computed Tomography (HRXCT) imagery. Cartilaginous and conspicuous bony structures were examined in cleared and double stained preparations of isolated head, branchial arch and pelvic girdle. Soft anatomy was examined by dissections, and in cleared and stained material. The HRXCT imagery is of a paratype (TNHC 29072) generated at the High-Resolution X-ray CT Facility at The University of Texas, Austin. The scanning parameters were as follows. A Feinfocus microfocal X-ray source operating at 120 kV and 0.2 mA with no X-ray prefilter was employed.

For each slice, 1000 views were taken with two samples per view. The field of image reconstruction was 73 mm, corresponding to a resolution of 71.3 microns per pixel for the 1024 by 1024 pixel slices. The specimen was scanned in multi-slice mode, in which 29 slices were collected simultaneously during a single specimen rotation resulting in a total of 1363 transverse (=coronal) CT slices. The scan was taken along the long axis of the specimen from the tip of the snout to the middle of the dorsal fin base. Visualizations were performed in the commercial software package VG Studio Max. Although the renderings appear similar to photographs, they represent the density differences of the biological materials as reflected in their X-ray opacity. Preparation of Figs. 4–7 utilized still frames captured from digital animations of HRXCT images with illustrations of soft anatomy overlain in Adobe®Photoshop®CS.

All digital source materials, including slice movies, digital reslicings, animations and figures, and an applet-based slice viewer are available at <http://digimorph.org> and <http://clade.acnatsci.org/catfishbone/>. Contact JMH for the 2.5 GB compressed file containing the original 16 bit slice data.

Metric and meristic characters generally follow Lundberg and McDade (1986) and Lundberg and Parisi (2002) with the following added: head depth at eye, head depth at occiput, eye to posterior margin of bony opercle, snout margin to anterior nostril, width of premaxillary tooth bands, lower jaw symphysis to gular fold, maxillary barbel length, nasal barbel length, outer mental barbel length, inner mental barbel length, width between inner mental barbels, width between outer mental barbels, posterior margin of bony opercle to dorsal fin, dorsal-spine length including flexible distal extension of ossified spine, longest (fourth) dorsal-fin ray, dorsal-fin end to adipose origin, pectoral-spine length including flexible distal part, longest (second) pectoral-fin ray, longest (third) pelvic-fin ray, width between pelvic-fin insertions, anal-fin to pelvic-fin origins, pectoral to pelvic-fin origins, anal-fin origin to anus, adipose-fin end to middle caudal-fin rays, middle caudal-fin rays, dorsal-fin to pectoral-fin origins, dorsal-fin to pelvic-fin origins, dorsal-fin end to pectoral-fin origin, dorsal-fin end to pelvic-fin origin, dorsal-fin end to anal-fin origin, adipose-fin to pelvic-fin origins, adipose-fin to anal-fin origins, adipose-fin origin to anal-fin end, adipose-fin end to anal-fin origin, adipose-fin to anal-fin ends.

Vertebral counts include 6 elements in the Weberian complex; the first caudal vertebra is that immediately posterior to visceral cavity; compound caudal vertebra (PU1 + U1) is counted as one. Dorsal-fin spine length, as well as counts of anal- and caudal-fin rays and vertebrae, was taken from x-ray images.

To provide a first evaluation of the phylogenetic placement of *Lacantunia* we examined it for possession of previously reported diagnostic synapomorphies of monophyletic siluriform clades at and above the family level. The clades and principal references are: Diplomystidae (Arratia 1987); Siluroidei (Grande 1987); Hypsidoridae (Grande 1987, Grande & de Pinna 1998); Cetopsidae (de Pinna & Vari 1995); Amphiliidae (Diogo 2003); Loricarioidei (Schaefer 1990, de Pinna 1992, de Pinna 1998); Nematogenyidae (de Pinna

1992, de Pinna 1998); Trichomycteridae (de Pinna 1992, de Pinna 1998); Callichthyidae (Reis 1998); Scoloplacidae (Schaefer 1990); Astroblepidae (Schaefer 1990); Loricariidae (Schaefer 1987, Armbruster 2004); Sisoroidei (de Pinna 1996, de Pinna & Ng 2004); Akysidae (de Pinna 1996); Amblycipitidae (Chen 1994, de Pinna 1996); Erethistidae (de Pinna 1996); Sisoridae (de Pinna 1996); Aspredinidae (Friel 1994, de Pinna 1996); Pseudopimelodidae (Lundberg *et al.* 1991a, Shibatta 1998); Heptapteridae (Lundberg & McDade 1986, Bockmann 1998); Pimelodidae (Nass 1991, Lundberg *et al.* 1991b); Doradoidei (Royero 1987, Ferraris 1988, de Pinna 1998); Mochokidae (Mo 1991, de Pinna 1993); Doradidae (Higuchi 1992); Auchenipteridae (Ferraris 1988); Ariidae (Mo 1991, Marceniuk 2003); Clariidae (Teugels & Adrians 2003); Schilbidae (Mo 1991, de Pinna 1993); Pangasiidae (de Pinna 1993); Claroteidae (Mo 1991); Australoglanididae (Mo 1991); Malapteruridae (Howes 1985, de Pinna 1993); Bagridae (Mo 1991, Ng 2003); Australoglanididae (Mo 1991); Cranoglanididae (Diogo *et al.* 2002); Ictaluridae (Lundberg 1982, Grande & Lundberg 1988, Lundberg 1992); Siluridae (Bornbusch 1991, Bornbusch 1995); Chacidae (Brown & Ferraris 1998, Diogo *et al.* 2004); Plotosidae (de Pinna 1993).



FIGURE 2. Deep pool habitat of *Lacantunia enigmatica* at El Remolino near the type locality on the Río Lacantún, April 2001, photo by H. Bahena. Insert: freshly collected specimen of *Lacantunia enigmatica* (TNHC 29071, collected in 1998, female, 347 SL) showing life coloration, in particular the brown gray ground color and light margins of the paired fins and gill cover membrane and maxillary barbels.

Order Siluriformes

Family Lacantuniidae n. fam. Rodiles-Hernández, Hendrickson & Lundberg

Diagnosis: As for the single contained genus *Lacantunia*, see below.

Remarks. Our creation of a monotypic family for *L. enigmatica* follows common practice in zoology and provides a name at that commonly used taxonomic rank for use in

lists and catalogues. An alternative convention in classification would be to list *L. enigmatica* as *Incertae Sedis* at the family rank.

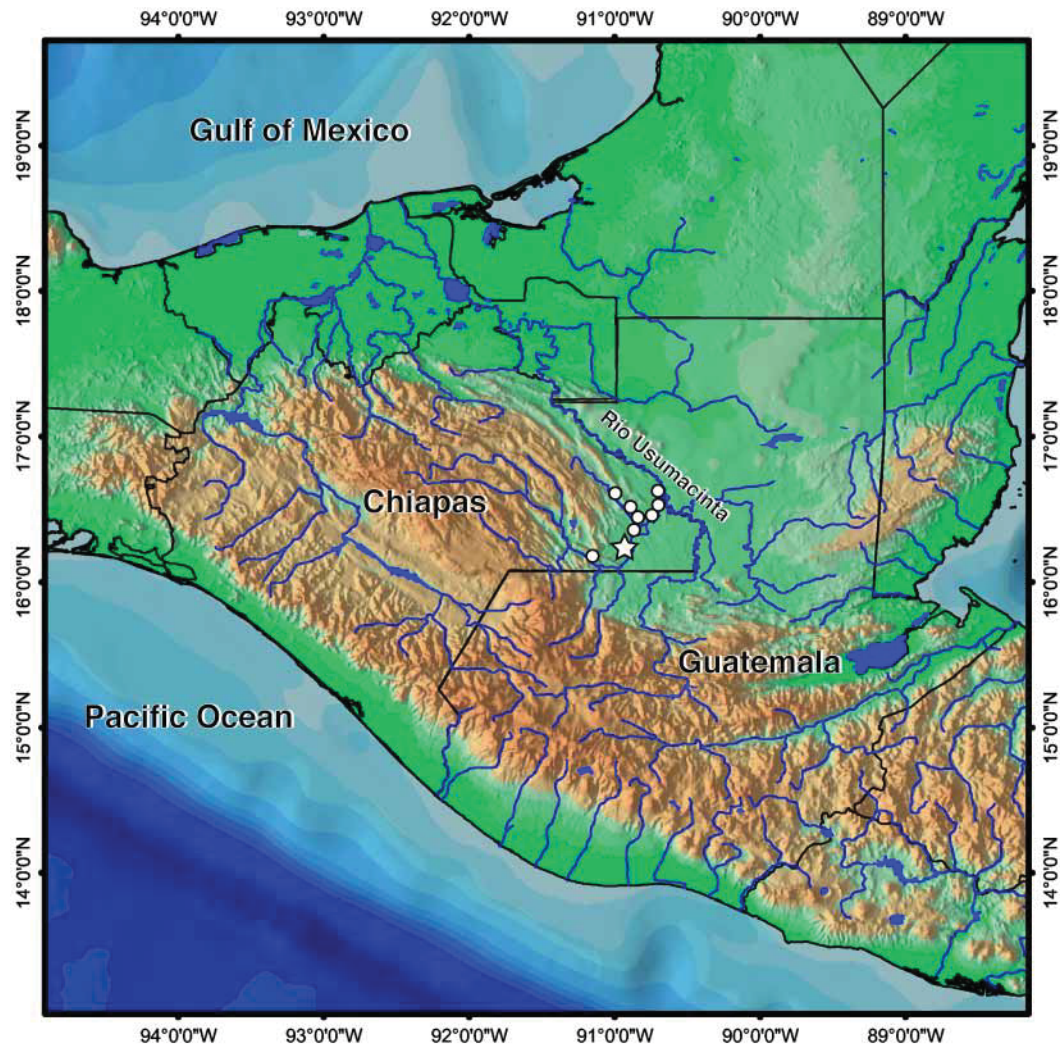


FIGURE 3. Map showing area of main collection localities of *Lacantunia enigmatica* in Chiapas, MX, star symbol indicates type locality (Diego M. Díaz Bonifaz, ECOSUR).

***Lacantunia* n. gen. Rodiles-Hernández, Hendrickson & Lundberg**

Figs. 1–2, 4–7

Type species. *Lacantunia enigmatica* n. sp.

Diagnosis: *Lacantunia* is distinguished from all other siluriforms by five uniquely derived and anatomically complex characteristics.

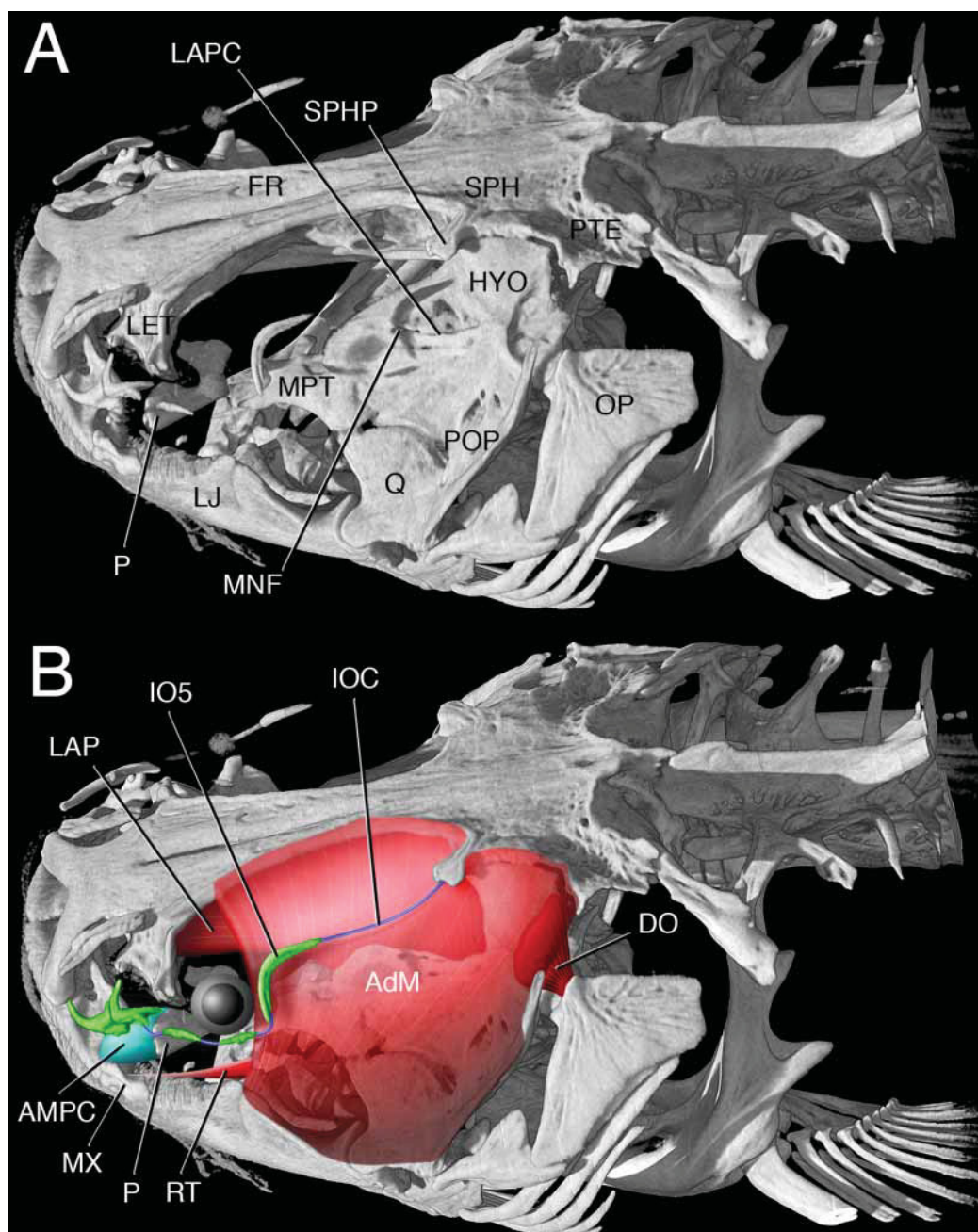


FIGURE 4. Cranial morphology of *L. enigmatica* based on HRXCT images of TNHC 29072, 223 mm SL. A. Dorsolateral view of skeleton of head, anterior vertebrae and pectoral girdle and fin. Abbreviations: FR frontal, HYO hyomandibula, LAPC levator arcus palatini crest, LET lateral ethmoid, LJ lower jaw, MNF mandibular nerve foramen, MPT metapterygoid, OP opercle, P palatine, POP preopercle, PTE pterotic, Q quadrate, SPH sphenotic, SPHP sphenotic process. B. Digital illustration of selected soft anatomical parts overlain on skeleton. Colors and abbreviations: Red muscle, Blue cartilage, Green infraorbital bones, Purple infraorbital sensory canal, Gray eye. AdM adductor mandibulae, AMPC anterior-medial palatine cartilage, DO dilatator operculi, IO5 fifth infraorbital, IOC infraorbital sensory canal, LAP levator arcus palatini, MX maxilla, RT retractor tentaculi.

- 1) Fifth infraorbital bone relatively wide and thick-walled, boomerang-shaped and anteriorly convex, and remote from a markedly prominent sphenotic process (Fig. 4). A long, naked span of the infraorbital sensory canal traverses the bone-free gap between IO5 and the sphenotic process. Primitively in catfishes the infraorbital sensory canal is almost completely surrounded by thin tubular ossicles separated by short gaps, the largest infraorbital bone (fifth or sixth) posterior to eye is simple and anteriorly concave, contacting or close to the sphenotic process that is small or lacking (Lundberg 1982, Mo 1991).
- 2) Lateral margin of skull thickened along frontal bone and adjacent parts of lateral ethmoid and sphenotic bones at origins of much enlarged adductor mandibulae and levator arcus palatini muscles (Fig. 4). Also, skull roof medial to muscle origins severely constricted, flat, lacking crests and fossae. Most catfishes have smaller jaw and hyoid arch muscles with limited cranial attachments (Lundberg 1982, Grande & de Pinna 1998) and broader, arched skull roofs across the frontals and sphenotics. Other catfishes with enlarged jaw and hyoid arch muscles (e.g. diplomystids, modern ictalurids, most cetopsids, some amblycipitids, bagrids, clariids and heptapterids) have different patterns of muscle arrangement and attachment sites dorsally on skull roof (Arratia 1987, de Pinna & Vari 1995, Grande & de Pinna 1998, Bockmann 1998).
- 3) Pair of cone-shaped "pseudo-pharyngobranchial" bones at anterior tips of enlarged accessory cartilages medial to first and second epibranchials (Fig. 5). Many catfishes have small, paired accessory cartilages medial to the cartilaginous caps on the epibranchials (Bockmann 1998), but without ossification. The "pseudo-pharyngobranchial" bones and accessory cartilages of *Lacantunia* are not homologous with first or second pharyngobranchials that are primitively retained in a few siluriforms as rod-shaped bones anteriorly adjacent and parallel to their companion epibranchials (Arratia 1987).
- 4) Hypertrophied, axe-shaped uncinat process on third epibranchial (Fig. 5). Primitively the third epibranchial of catfishes lacks an uncinat process. Some catfishes have a low process or, if enlarged, a process of markedly different shape (de Pinna 1993).
- 5) Gas bladder with paired spherical, unencapsulated diverticulae protruding from anterodorsal wall, each extending dorsad before anterior limb of fourth transverse process, lateral to first centrum and anterior limb of tripus, and posterior to occiput and ossified Baudelot's ligament (Fig. 6). Diverticulae walls of tough connective tissue containing silvery guanine crystals as in wall of main gas bladder chamber; without heavy vascularization. Catfishes primitively lack gas bladder diverticulae, though a few have different unpaired or multiple diverticulae posterior or lateral to main bladder (Chardon 1968).

Other characters useful for identification. Anterior and posterior nostrils widely separated (cf. nostrils adjacent in sympatric species of Ariidae); nasal barbel present on anterior rim of posterior nostril (cf. nasal barbel absent in sympatric species of Ariidae and Heptapteridae); maxillary barbel inserted above lip remote from corner of mouth (cf. max-

illary barbel inserted on corner of lip in sympatric species of Ictaluridae); upper lip without accessory folds parallel to premaxillary teeth (cf. upper lip with a fold parallel to premaxillary teeth in sympatric species of Heptapteridae); palate edentulous (cf. palate toothed in sympatric species of Ariidae); eye without a free orbital rim (cf. eye with a free orbital rim in sympatric species of Ictaluridae, Ariidae and Heptapteridae); supraoccipital process very short and remote from dorsal-fin base (cf. supraoccipital process projecting well beyond skull, often reaching dorsal-fin base in sympatric species of Ictaluridae, Ariidae and Heptapteridae); dorsal-fin soft rays 8 to 10 (cf. dorsal-fin soft rays 6 or 7 in sympatric species of Ictaluridae, Ariidae and Heptapteridae); pelvic rays 6 (cf. pelvic rays greater than 6 in sympatric species of Ictaluridae); caudal fin slightly rounded to truncate with rounded corners, its principal caudal rays 1,7,9,1 (cf. caudal fin distinctly lobed or forked, its principal caudal rays 1,7,8,1 in sympatric species of Ictaluridae and Heptapteridae, and 1,6,7,1 in Ariidae).

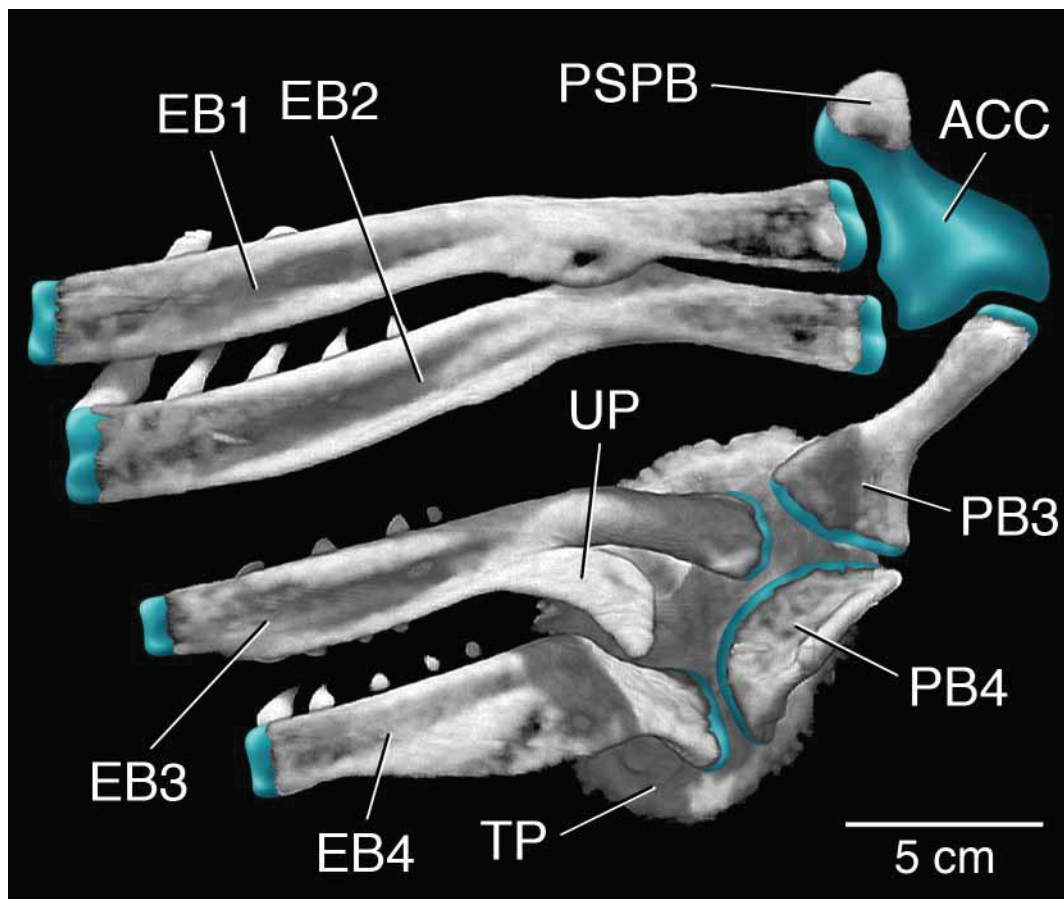


FIGURE 5. Dorsal view of digitally isolated left side branchial skeleton of *L. enigmatica*. Color and abbreviations: Blue cartilage, ACC accessory cartilage, EB1-4 epibranchials 1-4, PB3-4 pharyngobranchials 3-4, PSPB pseudo-pharyngobranchial, TP tooth plate, UP uncinate process.

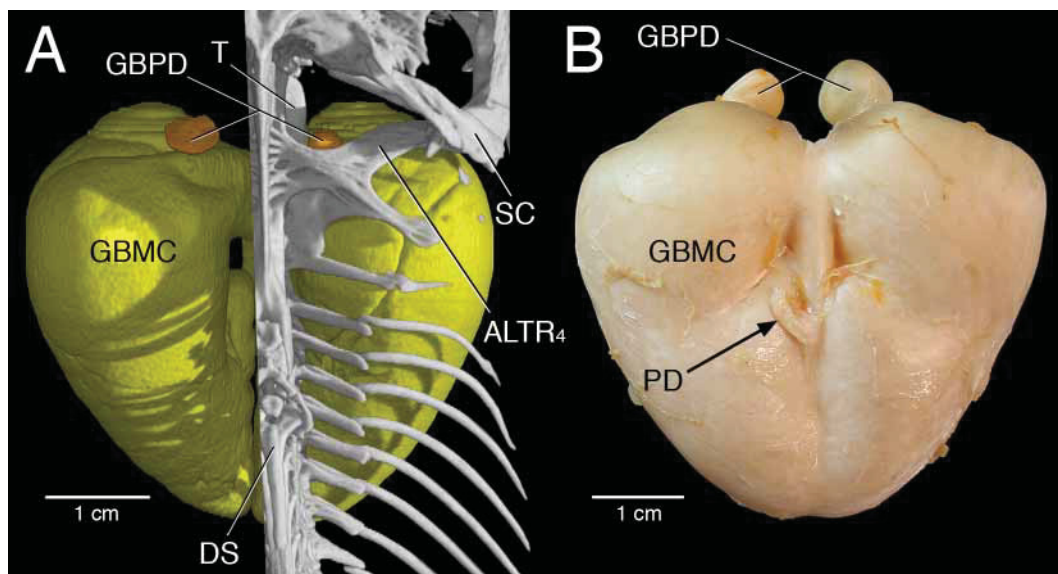


FIGURE 6. A. Anterior vertebrae (left side digitally removed) and gas-bladder morphology of *L. enigmatica* all based on HRXCT images. B. Ventral view of surface of an isolated gas bladder. Abbreviations: ALTR₄ anterior limb of 4th transverse process, DS dorsal-fin spine, GBMC gas bladder main chamber, GBPD gas bladder paired diverticulae, PD pneumatic duct, SC posttemporal-supracleithrum, T tripus.

Etymology. *Lacantunia*, from the Río Lacantún in Chiapas, the tributary river of Río Usumacinta inhabited by the new catfish, gender feminine.

***Lacantunia enigmatica* n. sp. Rodiles-Hernández, Hendrickson & Lundberg**

Table 1

Holotype. ECO-SC 3859 (Fig. 1), male, 427 mm SL, México, Chiapas, Río Usumacinta basin, Río Lacantún, Selva Lacandona, Reserva de la Biosfera Montes Azules, 16°08.083' N, 90°55.317' W (Fig. 3), Rodiles-Hernández, 8 November 2002.

Paratypes. All Chiapas, México, Río Usumacinta basin. Museum code (following Leviton *et al.* (1985) but adding here ECO-SC [ECOSUR San Cristóbal, address as for first author] and ENCB-IPN [Escuela Nacional de Ciencias Biológicas – Instituto Politécnico Nacional – address as for IPN in Leviton *et al.*]) and number is followed when data are available by sex, SL mm, collection date, Reserve (Reserva de la Biosfera Montes Azules = RIBMA; Selva Lacandona = SLac [Río Lacantún basin]), Municipio (Benemérito de las Américas [BA], Marqués de Comillas [MdC]), specific locality, Lat. N, Long. W, collector (CCS=Celedonio Chan-Salas; EVV=Ernesto Velázquez-Velázquez; SDC=Sara Domínguez-Cisneros; RRH=Rocío Rodiles-Hernández). * indicates articulated and disarticulated material; ** cleared and stained preparation; *** HRXCT data exam-

ined: ANSP 178696**, female, 280 mm, 14 May 1996, RIBMA, Río Lacanjá, 16° 25.92' N, 90° 51.8' W, RRH; ANSP 178697, female, 280 mm, 19 May 1997, RIBMA, Río Lacanjá, 16° 26.75' N, 90° 51.63' W, CCS; ANSP 178698*, male, 318 mm, 20 May 1997, SLac, MdC, Zamora Pico de Oro, 16° 20.10' N, 90° 50.58' W, RRH; ECO-SC 1166, female, 406 mm, 01 Mar. 1997, SLac, MdC, Zamora Pico de Oro, 16° 22.8' N, 90° 44.99' W, RRH; ECO-SC 3856, female, 384 mm, 20 May 2001, SLac, MdC, entre Reforma Agraria y Zamora Pico de Oro, 16° 20.10' N, 90° 50.58' W, RRH; ECO-SC 3858, male, 320 mm, 3 May 2002, SLac, MdC, Reforma Agraria, 16° 15.31' N, 90° 51.99' W, RRH; ENCB-IPN 5787, male, 353 mm, 20 May 1997, SLac, MdC, Zamora Pico de Oro, 16° 20.10' N, 90° 50.58' W, RRH; IBUNAM 12739, female, 282 mm, 20 May 2001, SLac, MdC, entre Reforma Agraria y Zamora Pico de Oro, 16° 15.31' N, 90° 51.99' W, RRH; TNHC 29071***, female, 347 mm, 5 Dec. 1998, SLac, BA, Puente Lacantún, 16° 32.45' N, 90° 41.7' W, EVV; TNHC 29072***, female, 223 mm, 20 May 1997, SLac, MdC, Zamora Pico de Oro, 16° 20.10' N, 90° 50.58' W, RRH; UANL 15259, female, 351 mm, 21 Aug. 1998, SLac, MdC, Río Chajulillo, 16° 5.57' N, 90° 57.47' W, EVV; UMMZ 243699, female, 295 mm, 20 Mar. 1997, RIBMA, Río Lacanjá, 16° 24.45' N, 90° 49.46' W, CCS; USNM 378035, male, 354 mm, 11 Dec. 1997, RIBMA, Río Lacanjá, 16° 25.525' N, 90° 50.986' W, EVV.

Non-type specimens of *Lacantunia enigmatica*. ANSP 178695, female, 330 mm, 21 Aug. 1998, SLac, MdC, Río Chajulillo, 16° 5.57' N, 90° 57.47' W, EVV; CAS 220134, female, 290 mm, 21 Sep. 1997, SLac, MdC, Ejido Reforma Agraria, 16° 15.31' N, 90° 51.99' W, CCS; ECO-SC 1239-2, male, 314 mm, 21 Sep. 1997, SLac, MdC, Ejido Reforma Agraria, 16° 15.31' N, 90° 51.99' W, CCS; ECO-SC 1363-3, female, 308 mm, 20 May 1997, SLac, MdC, Ejido Zamora Pico de Oro, 16° 20.10' N, 90° 50.58' W, RRH; ECO-SC 1368-2, 274 mm, 19 May 1997, RIBMA, Río Lacanjá, 16° 26.75' N, 90° 51.63' W, CCS; ECO-SC 1426, female, 319 mm, 19 May 1997, RIBMA, Río Lacanjá, 16° 26.94' N, 90° 51.84' W, EVV; ECO-SC 1511-2, female, 302 mm, 11 Dec. 1997, RIBMA, Río Lacanjá, 16° 25.525' N, 90° 50.986' W, EVV; ECO-SC 2138, male, 356 mm, 21 Mar. 1998, RIBMA, Río Lacanjá, 16° 24.581' N, 90° 49.502' W, EVV; ECO-SC 2582-1, male, 384 mm, 9 Sep. 1998, SLac, MdC, Arroyo Caribe, 16° 34.577' N, 90° 42.342' W, EVV; ECO-SC 2582-2, female, 344 mm, 9 Sep. 1998, SLac, MdC, Arroyo Caribe, 16° 34.577' N, 90° 42.342' W, EVV; ECO-SC 4005, 360 mm, 7 Feb. 2003, SLac, MdC, Reforma Agraria, 16° 15.31' N, 90° 51.99' W, CCS; ECO-SC 4006**, male, 370 mm, 15 May 2003, SLac, MdC, Reforma Agraria, 16° 15.31' N, 90° 51.99' W, CCS; ECO-SC 4008, female, 340 mm, 15 Jun. 1997, RIBMA, Río Tzendales, CCS; ECO-SC 4009**, female, 322 mm, 12 Jun. 1977, SLac, MdC, not specified, CCS; ECO-SC 4125, female, 340 mm, 24 Nov. 2003, SLac, MdC, Reforma Agraria, 16° 15.31' N, 90° 51.99' W, CCS; ECO-SC 4126, male, 330 mm, 30 Jan. 2004, SLac, MdC, Reforma Agraria, 16° 15.31' N, 90° 51.99' W, CCS.

Diagnosis: Same as genus.

Description: Maximum size exceeding 400 mm SL. Proportional measurements are given in Table 1. Body moderately elongate, markedly depressed anteriorly, strongly compressed posteriorly. Dorsal profile rises vertically from nearly terminal mouth on snout, then in a sharply convex curve from snout to above orbit, then straight and rising gently to occiput; most specimens with low nuchal hump before dorsal-fin origin; profile continuing horizontally below and behind dorsal fin to adipose-fin origin; falling gently below adipose to caudal-fin base. Ventral profile abruptly convex downward from mandible tip to mental barbels; gently convex or straight along head, pectoral girdle and abdomen to pelvic girdle; straight to anal-fin origin, finally rising in straight line to slightly concave curve to caudal-fin base.

TABLE 1. Measurement data for *Lacantunia enigmatica* holotype and 10 paratypes with standard length in mm and other measurements expressed in thousandths of standard length.

Measurement	Holotype	Mean	Range
Standard length	427	340	223–427
Prepectoral length	153	359	333–455
Predorsal length	109	255	225–339
Head length, bony	110	260	246–313
Head length, gill membrane	116	274	255–336
Head depth at eye	45	101	80–130
Head depth at occiput	54	119	94–161
Body depth at dorsal-fin origin	82	186	146–221
Posterior cleithral process	21	57	46–81
Caudal peduncle depth	43	106	95–140
Snout length	42	103	94–121
Eye diameter, horizontal	8	21	17–30
Eye diameter, vertical	7	18	15–28
Eye to posterior nostril	8	21	16–26
Bony interorbital	57	136	125–168
Eye to posterior margin of bony opercle	66	159	143–205
Snout to anterior nostril	10	26	21–34
Width between anterior nares	42	95	87–114
Width between posterior nares	44	101	92–128
Anterior to posterior nares distance	5	12	10–17
Gape width	72	184	164–234
Premaxillary width	32	75	60–99
Lower jaw to gular fold	28	60	57–69
Maxillary barbel length	120	323	279–462
Nasal barbel length	38	111	86–157

.....continued on the next page

TABLE 1 (continued)

Measurement	Holotype	Mean	Range
Outer mental barbel length	72	230	169–332
Inner mental barbel length	26	77	61–103
Width between inner mental barbel	31	79	68–96
Width between outer mental barbel	52	138	121–185
Posterior margin of bony opercle to dorsal-fin origin	59	137	127–167
Dorsal-spine length, bony	11	38	26–57
Dorsal-spine length, entire	54	140	119–179
Longest (4th) dorsal-fin ray	60	151	130–202
Dorsal-fin base	53	128	111–167
Dorsal-fin end to adipose-fin origin	100	197	135–262
Adipose-fin length	99	292	232–370
Adipose-fin height	15	39	31–55
Pectoral-spine length, bony	29	74	60–108
Pectoral-spine length, entire	57	142	132–179
Longest (2nd) pectoral-fin ray	65	157	145–215
Width at pectoral-spine insertions	100	238	219–278
Longest (3rd) pelvic-fin ray	51	129	116–170
Width between pelvic-fin insertions	50	116	105–151
Anal-fin to pelvic-fin origins	123	311	261–417
Pectoral-fin to pelvic-fin origins	77	181	146–252
Anal-fin height	51	136	112–175
Anal fin to anus	40	97	67–141
Urogenital papilla to anal fin	32	83	57–116
Caudal peduncle length	52	134	116–178
Anal-fin base	81	196	173–249
Adipose-fin end to middle caudal-fin rays	31	75	67–99
Length of middle caudal-fin rays	50	149	117–199
Dorsal-fin to pectoral-fin origins	87	212	198–260
Dorsal-fin to pelvic-fin origins	105	248	218–300
Dorsal-fin end to pectoral-fin origin	122	300	263–386
Dorsal-fin end to pelvic-fin origin	74	178	152–208
Dorsal-fin end to anal-fin origin	115	273	249–352
Adipose-fin to pelvic-fin origins	110	227	195–305
Adipose-fin to anal-fin origins	71	161	143–188
Adipose-fin origin to anal-fin end	88	250	206–312
Adipose-fin end to anal-fin origin	124	299	268–377
Adipose-fin to anal-fin ends	53	131	119–161

Cross-sectional shape flattened oval at vertical through middle of eye; head depth at mid-eye much less than head width at same level, about equal to distance between posterior nares, and contained 3 times in bony HL. Maximum body width across cleithra at pectoral spine insertions always greater than body depth, about 3.6–4.6 times in SL. Cross sectional shape becoming sub-quadrangular and deeper behind eye to pelvic-fin insertions, body depth about equal to width near posterior insertion of dorsal fin, increasingly compressed posteriorly onto laterally-flattened caudal peduncle and fin.

In dorsal and ventral views, snout very broad and bluntly rounded, projecting slightly beyond mandibular symphysis. Mouth scarcely subterminal, opening anteriorly; margins of closed mouth smoothly curved; no teeth exposed when mouth closed; rictus below eye; gape width about 1.3–1.6 in membranous HL; 1.8–2.1 in predorsal distance. Lips moderately papillate, more so in larger fish; lips set off by grooves from bands of jaw teeth and without accessory folds parallel to tooth rows. Fleshy rictal fold in a shallow pocket behind corner of mouth, protruding a little above general surface of head below maxillary barbel; ventral to rictal fold, a thin submandibular groove extends less than 1/2 distance to symphysis; dorsal to rictal fold a shallow groove extends anteriorly to terminate at insertion of maxillary barbel.

Each premaxillary tooth patch broad, its width about 3 times its symphyseal length; premaxillary teeth very fine, needle-like, tall and gently curved inward, especially the inner teeth; teeth arranged in irregular rows, about 18 teeth along transect near symphysis in specimens about 30 cm SL. Dentary teeth like those on premaxillary; tooth band broadest near symphysis, tapering laterally onto coronoid process. No teeth on palate.

Head skin thick, concealing skull roofing bones and narrowly open cranial fontanelles, yet skull roof near midline not buried by masses of jaw musculature dorsolaterally and laterally on head and masses of epaxial muscle on nape. Supraoccipital process not evident on surface behind occiput; process very short and remote from dorsal fin base.

Four pairs of proximally flattened barbels. Maxillary barbels inserted above lip midway between verticals through posterior nostril and eye; reaching to below dorsal fin. Maxillary barbels free from upper lip, laterally compressed basally, lying in shallow groove below eye and on cheek. Nasal barbel arises from anterior rim of posterior nostril; reaching a point 3–4 times eye diameter behind eye and about equal to distance between posterior nares. Inner mental barbels closer to margin of lower jaw than to gular fold apex, not reaching edge of gill membrane and about equal to or a little greater in length than distance between their bases. Outer mental barbels inserted at level of gular fold apex; tips of outer mental barbels reach onto depressed pectoral fin to a point slightly less than length of inner fin ray. Gular fold defining a deep groove in front of hyoid arch, its sides meeting apex at less than right angle. Gill membranes anteriorly united to each other, then diverging without overlap, supported by 11–12 branchiostegal rays (two on posterior ceratohyal, 1 or 2 on joint between ceratohyals, 8 on anterior ceratohyal). Gill rakers stiffly-ossified, sharp and slender; rakers on first branchial arch 14–15, (4 upper, 10–11 lower); first, sec-

ond and fifth branchial arches with single anterior rows of gill rakers, third and fourth arches with anterior and posterior rows.

Anterior nostril tubular, located dorsally on snout, remote from snout tip by about 3 times its own diameter, anterior to a line between anterior edges of maxillary barbel bases. Posterior nostril as close to anterior nostril as to eye (ca. twice its own diameter in front of eye); medially offset from a line between midpoint of anterior border of eye and anterior nostril; nostril rim a thin, hyaline membrane low or incomplete posteriorly and produced anteriorly as thick nasal barbel; aperture ovoid with its long axis parallel to longitudinal body axis.

Eye dorsolateral, centered on a vertical at about first third of bony HL, without a free orbital rim, clear corneal skin defines ocular surface and shape of eye. Ocular surface ovoid to nearly circular; pupil less than 50% of ocular surface. Eye relatively small: horizontal ocular diameter 11.2–14.2 in HL, 5.6–7.5 in interocular, 4–6.3 in snout.

Cephalic sensory canals thin; supratemporal, supraorbital, infraorbital, and preopercular canals lead to short, multiple-branched cutaneous canals and clusters of small pores on sides and top of head; cutaneous canal branches of mandibular and nasal canals not dendritic on chin and snout, respectively. Lateral line canal straight and superficial with simple, short tubes and pores, ending over hypurals.

Dorsal fin inserted a little anterior of first third of SL; its origin near a vertical at tip of inner pectoral-fin rays. 10–12 dorsal-fin rays: spinelet, spine, and 8–10 soft, branched rays; 9–11 pterygiophores. Dorsal-fin base embedded in thick tissue especially at its anterior insertion. Spinelet small, with a shallow anteromedial cavity and its limbs widely diverging at ca. 60° angle. Dorsal spine short, slender, straight, not denticulate; ossified for about half its length, otherwise segmented. Distal margin of dorsal fin rounded, second-fourth soft rays longest, last dorsal-fin ray more than 2/3 length of second soft ray.

Adipose fin large, thick; its anterior insertion at about 70% of SL, remote from dorsal fin base, by about 1.1–1.8 times dorsal base. Adipose-fin margin gently rounded, its apex at a vertical just behind middle of anal fin, ending without a short, free lobe at a weak notch in front of upper caudal fin lobe. Adipose-fin length 2.7–3.8 in SL, about 0.8–1 in HL, 2.2–2.7 in length of dorsal-fin base and 1.3–1.8 in length of anal-fin base; adipose-fin height 6–12 times in adipose fin length, 1.7–4.5 in least caudal peduncle depth.

Caudal fin slightly rounded to truncate with rounded corners. Principal caudal rays 1,7,9,1; 10–12 upper and 11–13 lower procurent caudal-fin rays.

Anal fin inserted a little behind a vertical at adipose fin origin; fin margin rounded; middle rays the longest. Anal-fin rays 22–26 (9–10 simple). Last two anal-fin rays closely separate; 22–25 anal-fin pterygiophores. Anal-fin base embedded in thick tissue especially at its anterior insertion.

Pectoral fin with a spine and 10–11 branched rays; its margin gently rounded, third soft ray longest; no fleshy membrane along medial edge of inner ray; depressed pectoral fin reaches to a vertical between second and third dorsal-fin soft rays. Pectoral spine

formed from basal half of first lepidotrich; distal half filamentous and segmented. Pectoral spine articulating base with typical siluriform dorsal, anterior and ventral processes. Shaft of spine without dentations or serrae, and terminating bluntly at transition to segmented ray.

Posterior cleithral process narrow, short and moderately sharp; surface buried in skin and weakly ornamented with few subparallel ridges. Axillary pore below postcleithral process.

Pelvic fin inserted a little behind a vertical at middle body and below midpoint of depressed last dorsal-fin ray; containing 6 rays, first simple, third longest; no fleshy membrane along medial edge of inner ray; pelvic-fin margin gently rounded; pelvic-fin length contained 6–8 times in SL and separated from anal-fin origin by half its length. Pelvic splint absent.

Total vertebrae 55–57, 22–25 precaudals and 31–33 caudals. Weberian complex including 6 vertebrae, first rib on sixth vertebra.

Urogenital papilla located in a shallow depression immediately behind anus between pelvic fins about midway along length of inner fin rays. No apparent sexual dimorphism. Distance from anus to anal fin origin about equal to length of inner pelvic ray.

Pigmentation. Back, upper sides, nape, and tympanic area laterally over swim bladder medium to dark brown in life and in alcohol pale to dark gray or grayish blue. Upper sides with small dark and irregularly scattered freckles or spots that fade in larger fish; no stripes. Lower sides and venter much lighter, cream to white anteriorly changing to light to medium gray posterior to anus and urogenital papilla or at anal-fin origin.

Dorsal fin with or without dark margin, and darker pigment concentrated in membranes between fin rays. Caudal and anal fins with broad dark margins. Adipose pigmentation like that of adjacent back and sides, with vague freckles or spots. Pectoral and pelvic fins with dorsal surfaces mostly pigmented brown to gray proximally; anterior and distal margins pallid, often strikingly so; ventral surfaces of both paired fins lighter; some individuals with evenly dark pectoral and pelvic fins.

Dorsum of head and opercles (except for light membranous margin) nearly uniform brown in life or dark gray in alcohol; no light spots over cranial fontanelles. Maxillary barbels dusky gray dorsally; often much lighter anteriorly and ventrally; increasingly lighter distally. Nasal barbels gray proximally grading to lighter tips. Membranous rim of posterior naris and tubular rim of anterior naris white. Lower sides and venter of head and inner mental barbels light cream to white. Outer mental barbels proximally with dark posterior edge, lighter distally.

Additional descriptive information on *L. enigmatica*, including video animations from high-resolution X-ray computed tomography (HRXCT) is available at <http://www.digimorph.org> and <http://clade.acnatsci.org/catfishbone/>.

Distribution and habitat. *Lacantunia enigmatica* occurs in the Ríos Lacantún and Lacanjá, tributaries of Río Usumacinta basin, Chiapas, México, inhabiting deep (to 18 m)

river channels and pools with rocks and strong eddy currents. Few specimens were taken in stream mouths. Specimens were collected in both high and low water seasons, and generally during the night. Gut contents include fishes, crabs, prawns and large, tough seeds.

Etymology. The name *enigmatica* is Latin for baffling or inexplicable in reference to the unexpected discovery, obscure relationships and origin of the new catfish. We suggest the common name “Chiapas Catfish” (= “Bagre de Chiapas”) for *L. enigmatica*.

Discussion

The major phylogenetic lines of Siluriformes are unevenly resolved. South American Diplomystidae are the sister-group to all other catfishes or Siluroidei (Grande 1987, Arratia 1987). The North American fossil Hypsidoridae (Grande 1987) are a deep clade subtending the remaining extant siluroid catfishes. The Neotropical extant Cetopsidae may also be among the most basal catfish lines (de Pinna & Vari 1995). The many remaining catfishes are placed in 31 well-supported, monophyletic families, yet few multi-family groups (Arratia *et al.* 2003). Phylogenetic resolution is high within many families (de Pinna 1993, Arratia *et al.* 2003), whereas most family interrelationships remain to be determined.

Lacantunia is not a basal catfish within or below Diplomystidae. Instead, the new catfish shares derived characters uniting all non-diplomystid catfishes into the Siluroidei (Grande 1987). These synapomorphies are: 8 upper principal caudal-fin rays (cf. primitively 9 in diplomystids); barbels on the chin (cf. no mental barbels); fifth vertebra sutured to compound second-fourth (Weberian) fused vertebrae and partly covered by lamellar bone (cf. fifth vertebra with non-sutural joints and lacking covering of lamellar bone). In Siluroidei, *Lacantunia* and non-hypsidorid catfishes share a reduced distal maxillary arm and short medial maxillary process (cf. in diplomystids and hypsidorids maxillary arm primitively expanded and maxillary process elongated), loss of maxillary teeth (cf. teeth present), and sutures uniting anterior and posterior ceratohyals (cf. synchondral joint between ceratohyals (Grande 1987, de Pinna 1993)). Also among Siluroidei, the development of interdigitating coracoid symphyseal sutures places *Lacantunia* with non-cetopsid as well as non-diplomystid catfishes (cf. primitively in diplomystids and cetopsids coracoid symphyseal sutures not present; although the sutures secondarily lost in Siluridae and some Trichomycteridae) (de Pinna 1993, de Pinna & Vari 1995).

Other Río Usumacinta basin catfishes belong to three families: Ictaluridae, Heptapteridae and Ariidae. Discovery of a new catfish belonging to any of these families would be unsurprising, but such is not the case. *Lacantunia* resembles ictalurids more than it does heptapterids or ariids, however, *Lacantunia* lacks the synapomorphies uniting crown group Ictaluridae (Lundberg 1982, Lundberg 1992, Grande & de Pinna 1998): skull roof covered by jaw adductor muscles attached to prominent sagittal crest (cf. primitively, as in *Lacantunia*, muscles not on skull roof and sagittal crest not developed); infraorbital canal

exits frontal bone (cf. canal exits sphenotic); supracleithrum with subpteroic process (cf. process absent). *Lacantunia* also lacks synapomorphies that place the fossil genus *Astephus*, an early Tertiary North American catfish, as the sister lineage to crown group Ictaluridae (Lundberg 1992, Grande & de Pinna 1998): loss of bony posterior process on pelvic girdle (cf. primitively ossified posterior process present as in *Lacantunia*); continuous cartilage along posterior edge of pelvic girdle (cf. cartilage in two parts interrupted by bone); pelvic-fin rays 7 or more and intraspecifically variable (cf. pelvic-fin rays invariably 6). We found no characters suggesting a deeper sister group relationship between *Lacantunia* and all Ictaluridae.

Lacantunia also lacks synapomorphies of Heptapteridae and Ariidae. Heptapterids (Bockmann 1998, Bockmann & Guazzelli 2003) are diagnosed by laterally branched fourth transverse vertebral processes (cf. transverse processes primitively unbranched as in *Lacantunia*); expanded posterodorsal projections of hyomandibula for insertion of levator operculi muscle (cf. process small); hyomandibula and metapterygoid not meeting dorsal to quadrate (cf. hyomandibula and metapterygoid in contact); recurved processes of ventrolateral corners of mesethmoid (cf. processes absent). Ariidae (Mo 1991, Marceniuk 2003) have a unique otic capsule with a distended bulla involving the prootic, pterotic and exoccipital bones that houses an enlarged utricular otolith (cf. primitively otic bulla absent and otolith small as in *Lacantunia*).

Some presumably derived characters shared by *Lacantunia* and various non-hypsirodon siluroids were found. However, without supporting evidence these are not interpreted as unambiguous synapomorphies for placing the new catfish within, or as the sister lineage to, any recognized siluroid subgroup. In previous studies done without *Lacantunia*, many of these putatively derived characters were interpreted as homoplasious similarities among different catfish groups. For example, the palatine bones of Cetopsidae (de Pinna & Vari 1995), some Claroteidae (Mo 1991) and *Lacantunia* are similarly truncated anteriorly with enlarged anterior palatine cartilages extended medially onto the lateral ethmoid condyle (Figs. 4A, 7). Siluroids primitively have a more elongate palatine with a small anterior cartilage separate from the lateral ethmoid condyle. Based on character evidence more strongly favoring alternative relationships, de Pinna and Vari (1995) concluded that the palatine condition of cetopsids and claroteids evolved independently. We tentatively identify the palatine condition of *Lacantunia* as independently derived relative to these other catfish families.

Among the most evident, widely shared derived feature found in *Lacantunia* and several siluroid taxa are the nasal barbels on the posterior nares (Fig. 1A, C). Posterior nasal barbels are not simple flaps of skin, but contain supportive elastocartilage cores on a cartilage base (Joyce & Chapman 1978). Absence of nasal barbels in diplomystids and cetopsids indicates that these structures evolved within siluroids, however, no Neotropical catfishes or ariids have posterior nasal barbels, and they are lacking in Old World Amphiliidae, Australoglanididae, Auchenoglanidinae, Chacidae, Malapteruridae, Mochokidae,

Pangasiidae and Siluridae. Posterior nasal barbels are present in *Lacantunia*, Ictaluridae, and Old World Bagridae, Claroteidae, Cranoglanididae, Schilbidae, Plotosidae, Clariidae, Amblycipitidae, Akysidae, Sisoridae and Erethistidae. Our phylogenetic analysis does not identify these taxa as a monophyletic group, but indicates homoplasy of nasal barbel evolution among siluroids.

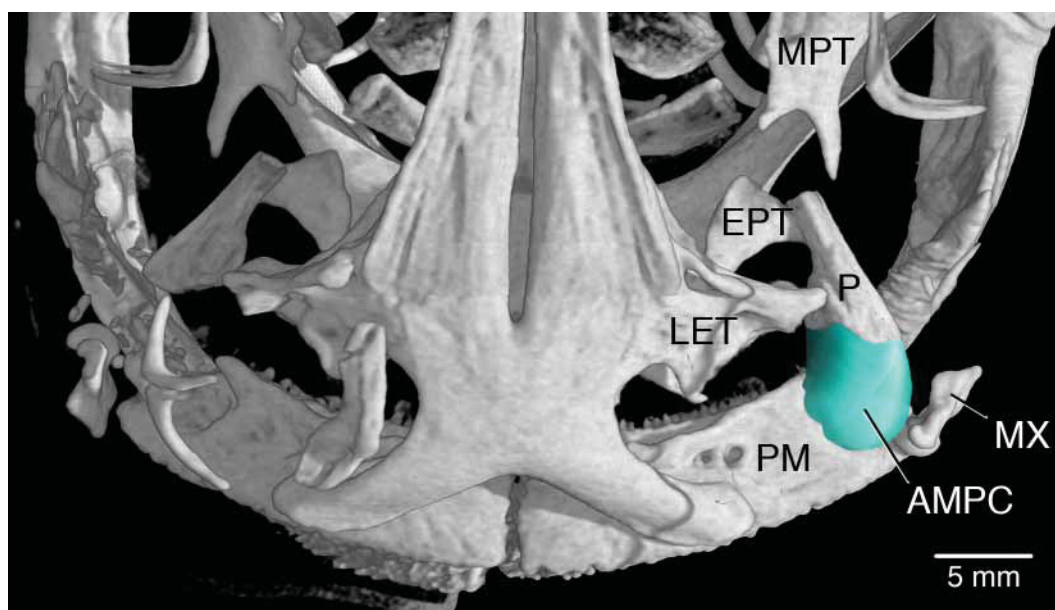


FIGURE 7. Anterodorsal view of head skeleton (left nasal and infraorbital bone 1 digitally removed) of *L. enigmatica* (TNHC 29072, 223 mm SL) based on HRXCT images. Colors and abbreviations: Blue cartilage. AMPC anterior-medial palatine cartilage, EPT endopterygoid, LET lateral ethmoid, MPT metapterygoid, MX maxilla, P palatine, PM premaxilla.

This first assessment, therefore, places *Lacantunia* above diplomystids, hypsidorids and cetopsids, but unresolved among the remaining monophyletic subgroups of siluroids. As shown by late Campanian to early Maastrichtian fossils of Diplomystidae, Ariidae and Doradoidei (Lundberg 1998, Gayet & Meunier 2003), diversification of modern catfishes was underway by late Cretaceous. Fossils also demonstrate that by at least Paleocene or Eocene several other catfish families and higher groups had originated: extinct Hypsidoridae, and modern Callichthyidae, Pimelodidae, Clariidae, Claroteidae, Bagridae, and Ictaluridae (Lundberg 1975, Grande 1987, Grande & de Pinna 1998, Lundberg 1998, Gayet & Meunier 2003). Significantly, some of these indicate coexistence of related “ghost” lineages yet unrecorded by fossils. For example, late Paleocene fossils of *Corydoras*, a living callichthyid genus, imply coeval or prior origins of confamilial genera and of other groups of Loricarioidei (Lundberg 1998, Reis 1998). A comparable early Tertiary

age seems possible for distinctive, yet unresolved, siluroid lineages such as *Lacantunia* if these are basal relatives to any single or multi-family clades. These suggestions are testable as more is learned about the interrelationships of catfishes.

Mesoamerica is famous for its complex yet elusive biogeographic and geologic histories (Raven & Axelrod 1979, Savage 1982). The biota of Central America and México is largely composed of plants and animals with separate extralimital affinities and differing inferred ages of origin (Raven & Axelrod 1979, Savage 1982, Wendt 1998). Biogeographers have drawn on the region's rich biota to illustrate or postulate post Late Cretaceous vicariance, endemic diversification and dispersal from North and South America, Caribbean islands and suspect accretionary terranes (Myers 1966, Savage 1982, Humphries 1982, Rosen 1985, Stehli & Webb 1985, Dickinson & Lawton 2001, Miller *et al.* in press). Nowhere is this broad biotic mix better exemplified than in the Río Usumacinta, where a highly endemic, apparently long-isolated, aquatic biota consists of species with North American affinity (e.g. ictalurid catfishes, catostomid suckers, dermatemydid turtles) living alongside others with South American relationships (heptapterid catfishes, characins, electric knife fish, cichlids), as well as some with deeper Afro-Indo-southeast Asian affinities (genus *Ophisternon* of Synbranchidae (Rosen 1975)). The Usumacinta also harbors several resident freshwater representatives of Atlantic coastal groups (ariids and gobioids), and many species belonging to species-rich endemic clades in groups such as poeciliids (Rodiles-Hernández in press), with deeper and less obvious geographic affinities.

Lacantunia enigmatica thus adds a fourth catfish clade to the Mesoamerican aquatic fauna. This biogeographically puzzling species shows no close relationship to any North or South American or marine taxon, as do the other Usumacinta siluriforms. Without a clearly identified and geographically proximate relative, a hypothesis to consider is that *Lacantunia* represents an ancient and basal siluroid lineage from which intermediate members have disappeared. The phylogenetic resolution needed for more definitive dating and biogeographic placement of *Lacantunia* will require additional evidence, including both molecular and additional morphological characters.

As enigmatic as any evolutionary question raised by *Lacantunia* is its late ichthyological discovery. How was such a large and conspicuous species missed until now? Whatever the reasons, *Lacantunia* reminds us that the most basic scientific inventory of Earth's biodiversity is woefully incomplete. Unfortunately, this fascinating, enigmatic and geographically restricted taxon is acutely threatened by anthropogenic activities including forest removal, proposed hydroelectric reservoirs, and introductions of non-native taxa. Conservation of this unique organism should be a high priority for regional natural resource biodiversity conservation and management planners.

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References

- All Catfish Species Inventory Project (2004) *All Catfish Species Inventory Website*. Available from <http://clade.acnatsci.org/allcatfish/> (accessed 22 February 2005).
- Armbruster, J.W. (2004) Phylogenetic relationships of the suckermouth armoured catfishes (Loricariidae) with emphasis on the Hypostominae and the Ancistrinae. *Zoological Journal of the Linnean Society*, 141, 1–80.
- Arratia, G. (1987) Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. *Bonner Zoologische Monographien*, 24, 1–120.
- Arratia, G., Kapoor, B.G., Chardon, M. & Diogo, R. (2003) *Catfishes*. Science Publishers, Inc., Enfield, NH, USA, 812 pp.
- Bockmann, F.A. (1998) *Análise Filogenética da Família Heptapteridae (Teleostei, Ostariophysi, Siluriformes) e Redefinição de Seus Gêneros*, Ph.D. thesis Universidade de São Paulo, São Paulo, Brazil, 599 pp.
- Bockmann, F.A. & Guazzelli, G.M. (2003) Heptapteridae. In: Reis, R.E., Kullander, S.O. & Ferraris, C.J. (Eds.) *Check List of the Freshwater Fishes of South and Central America*. EDIPU-CRS, Porto Alegre, Brazil, pp. 406–431.
- Bornbusch, A.H. (1991) Monophyly of the catfish family Siluridae (Teleostei: Siluriformes), with a critique of previous hypotheses of the family's relationships. *Zoological Journal of the Linnean Society*, 101, 105–120.
- Bornbusch, A.H. (1995) Phylogenetic relationships within the Eurasian catfish family Siluridae (Pisces: Siluriformes), with comments on generic validities and biogeography. *Zoological Journal of the Linnean Society*, 115, 1–46.
- Brown, B.A. & Ferraris, C.J. (1998) Comparative osteology of the Asian catfish family Chacidae, with the description of a new species from Burma. *American Museum Novitates*, 2907, 1–16.
- Chardon, M. (1968) Anatomie comparée de l'appareil de Weber et des structures complexes chez les Siluriformes. *Annales du Musée Royal de l'Afrique Centrale, Tervuren, Belgique*, 169, 1–273.
- Chen, X. (1994) *Phylogenetic Studies of the Amblycipitid Catfishes (Teleostei, Siluriformes) With Species Accounts*, Ph.D. thesis Duke University, Raleigh-Durham, North Carolina, USA, 471 pp.
- Dickinson, W.R. & Lawton, T.F. (2001) Carboniferous to Cretaceous assembly and fragmentation

- of Mexico. *Geological Society of America Bulletin*, 113, 1142–1160.
- Diogo, R. (2003) Higher-level phylogeny of Siluriformes: an overview. *In*: Arratia, G., Kapoor, B. G., Chardon, M. & Diogo, R. (Ed) *Catfishes*. Science Publishers, Inc., Enfield, NH USA and Plymouth, UK, pp. 353–384.
- Diogo, R., Chardon, M. & Vandewalle, P. (2002) Osteology and myology of the cephalic region and pectoral girdle of the Chinese catfish *Cranoglanis boudierius*, with a discussion on the autapomorphies and phylogenetic relationships of the Cranoglanididae (Teleostei: Siluriformes). *Journal of Morphology*, 253, 229–242.
- Diogo, R., Chardon, M. & Vandewalle, P. (2004) On the osteology and myology of the cephalic region and pectoral girdle of *Chaca bankanensis* Bleeker 1852, with comments on the autapomorphies and phylogenetic relationships of the Chacidae (Teleostei: Siluriformes). *Animal Biology*, 54, 159–174.
- Eschmeyer, W.N. (1998) *Catalog of Fishes*. California Academy of Sciences, San Francisco, USA, 2905 pp.
- Ferraris, C.J. (1988) *The Auchenipteridae: Putative Monophyly and Systematics, with a Classification of the Neotropical Doradoid Catfishes (Ostariophysi, Siluriformes)*, Ph.D. thesis City University of New York, New York, USA, 229 pp.
- Friel, J.P. (1994) *A Phylogenetic Study of the Neotropical Banjo Catfishes (Teleostei: Siluriformes: Aspredinidae)*, Ph.D. thesis Duke University, Raleigh-Durham, North Carolina, USA, 256 pp.
- Gayet, M. & Meunier, F.J. (2003) Palaeontology and palaeobiogeography of catfishes. *In*: Arratia, G., Kapoor, B. G., Chardon, M. & Diogo, R. (Ed) *Catfishes*. Science Publishers, Inc., Enfield, NH USA and Plymouth, UK, pp. 491–522.
- Grande, L. (1987) Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes) with a reassessment of its phylogenetic relationships. *Journal of Vertebrate Paleontology*, 7, 24–54.
- Grande, L. & de Pinna, M.C.C. (1998) Description of a second species of the catfish †*Hypsidorus* and a reevaluation of the genus and the family †Hypsidoridae. *Journal of Vertebrate Paleontology*, 18, 451–474.
- Grande, L. & Lundberg, J.G. (1988) Revision and redescription of the genus *Astephus* (Siluriformes: Ictaluridae) with a discussion of its phylogenetic relationships. *Journal of Vertebrate Paleontology*, 8, 139–171.
- Higuchi, H. (1992) *A Phylogeny of the South American Thorny Catfishes (Osteichthyes; Siluriformes, Doradidae)*, Ph.D. thesis Harvard University, Cambridge, Massachusetts, USA, 372 pp.
- Howes, G.J. (1985) The phylogenetic relationships of the electric catfish family Malapteruridae (Teleostei: Siluroidei). *Journal of Natural History*, 19, 37–67.
- Humphries, C.J. (1982) Vicariance biogeography in Mesoamerica. *Annals of the Missouri Botanical Garden*, 69, 444–463.
- Joyce, E.C. & Chapman, G.B. (1978) Fine structure of the nasal barbel of the channel catfish, *Ictalurus punctatus*. *Journal of Morphology*, 158, 109–154.
- Leviton, A.E., Gibbs, R.H.J., Heal, E. & Dawson, C.E. (1985) Standards in herpetology and ichthyology: Part 1. Standard symbolic codes and institutional resource collections in herpetology and ichthyology. *Copeia*, 1985, 802–832.
- Lundberg, J.G. (1975) The fossil catfishes of North America. *University of Michigan Papers on Paleontology*, 2, 1–51.
- Lundberg, J.G. (1982) The comparative anatomy of the toothless blindcat, *Trogloglanis pattersoni* Eigenmann, with a phylogenetic analysis of the ictalurid catfishes. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 163, 1–83.
- Lundberg, J.G. (1992) The phylogeny of ictalurid catfishes: A synthesis of recent work. *In*: Mayden, R. L. (Ed) *Systematics, Historical Ecology, and North American Freshwater Fishes*. Stanford University Press, Stanford, California, USA, pp. 392–420.

- Lundberg, J.G. (1998) The temporal context for diversification of neotropical fishes. *IN: Malabarba, L. R., Reis, R. E., Vari, R. P., Lucena, C. A. S. & Lucena, Z. M. S. (Ed) Phylogeny and Classification of Neotropical Fishes*. Museu de Ciencias e Tecnologia, PUCRS, Porto Alegre, Brazil, 49–68.
- Lundberg, J.G., Bornbusch, A.H. & Mago-Leccia, F. (1991a) *Gladioglanis conquistador* N. Sp. from Ecuador with diagnoses of the subfamilies Rhamdiinae Bleeker and Pseudopimelodinae N. Subf. (Siluriformes: Pimelodidae). *Copeia*, 1991, 190–209.
- Lundberg, J.G., Kottelat, M., Smith, G.R., Stiassny, M.L.J. & Gill, A.C. (2000) So many fishes, so little time: An overview of recent ichthyological discovery in continental waters. *Annals of the Missouri Botanical Garden*, 87, 26–62.
- Lundberg, J.G., Mago-Leccia, F. & Nass, P. (1991b) *Exallodontus aguanai*, a new genus and species of Pimelodidae (Pisces: Siluriformes) from deep river channels of South America, and delimitation of the subfamily Pimelodinae. *Proceedings of the Biological Society of Washington*, 104, 840–869.
- Lundberg, J.G. & McDade, L.A. (1986) A redescription of the rare Venezuelan catfish *Brachyrhamdia imitator* Myers (Siluriformes: Pimelodidae) with phylogenetic evidence for a large intrafamilial lineage. *Notulae Naturae*, 463, 1–24.
- Lundberg, J.G. & Parisi, B.M. (2002) *Propimelodus*, new genus, and redescription of *Pimelodus eigenmanni* Van der Stigchel 1946, a long-recognized yet poorly known South American catfish (Pimelodidae, Siluriformes). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 152, 75–88.
- Marceniuk, A.P. (2003) *Relações Filogenéticas e Revisão dos Gêneros da Família Ariidae (Ostariophysi, Siluriformes)*, Ph.D. thesis Universidade de São Paulo, Brazil, 256 pp.
- Miller, R.R., Minckley, W.L. & Norris, S.M. (in press) *Freshwater Fishes of Mexico*. University of Chicago Press, Chicago, Illinois, USA.
- Mo, T.-P. (1991) Anatomy and systematics of Bagridae (Teleostei) and siluroid phylogeny. *Theses Zoologicae*, 17, 1–216.
- Myers, G.S. (1966) Derivation of the freshwater fish fauna of Central America. *Copeia*, 4, 766–773.
- Nass, P. (1991) *Anatomía Comparada del Bagre Cunagaro Brachyplatystoma juruense (Boulenger, 1898), Incluyendo un Analisis Filogenético de la Familia Pimelodidae*, Ph.D. thesis Universidad Central de Venezuela, Caracas, 262 pp.
- Ng, H.H. (2003) Phylogeny and systematics of Bagridae. *IN: Arratia, G., Kapoor, B. G., Chardon, M. & Diogo, R. (Ed) Catfishes*. Science Publishers, Inc., Enfield, NH USA and Plymouth, UK, 439–463.
- de Pinna, M.C.C. (1992) A new subfamily of Trichomycteridae (Teleostei, Siluriformes), lower loricarioid relationships and a discussion on the impact of additional taxa for phylogenetic analysis. *Zoological Journal of the Linnean Society*, 106, 175–229.
- de Pinna, M.C.C. (1993) *Higher-Level Phylogeny of Siluriformes (Teleostei, Ostariophysi), With a New Classification of the Order*, Ph.D. thesis City University of New York, New York, USA, 482 pp.
- de Pinna, M.C.C. (1996) A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae, and Amblycipitidae, with a hypothesis on the relationships of the neotropical Aspredinidae (Teleostei, Ostariophysi). *Fieldiana (Zoology)*, 84, 1–83.
- de Pinna, M.C.C. (1998) Phylogenetic relationships of neotropical Siluriformes (Teleostei: Ostariophysi): historical overview and synthesis of hypotheses. *IN: Malabarba, L. R., Reis, R. E., Vari, R. P., Lucena, Z. M. S. & Lucena, C. A. S. (Ed) Phylogeny and Classification of Neotropical Fishes*. EDIPUCRS, Porto Alegre, Brazil, pp. 279–330.
- de Pinna, M.C.C. & Ng, H.H. (2004) The second ural centrum in Siluriformes and its implication for the monophyly of superfamily Sisoroidea (Teleostei, Ostariophysi). *American Museum Novitates*, 3437, 1–23.

- de Pinna, M.C.C. & Vari, R.P. (1995) Monophyly and phylogenetic diagnosis of the family Cetopsidae, with synonymization of the Helogenidae (Teleostei: Siluriformes). *Smithsonian Contributions to Zoology*, 57, 1–26.
- Raven, P.H. & Axelrod, D.I. (1979) Angiosperm biogeography and past continental movements. *Annals of the Missouri Botanical Garden*, 61, 539–673.
- Reis, R.E. (1998) Systematics, biogeography, and the fossil record of the Callichthyidae: a review of the available data. *IN*: Malabarba, L. R., Reis, R. E., Vari, R. P., Lucena, Z. M. S. & Lucena, C. A. S. (Ed) *Phylogeny and Classification of Neotropical Fishes*. EDIPUCRS, Porto Alegre, Brazil, pp. 351–362.
- Rodiles-Hernández, R. (in press) Diversidad de peces continentales en Chiapas, México. *IN*: González-Espinosa, N., Ramírez-Marcial, N. & Ruiz-Montoya, L. (Ed) *Diversidad Biológica de Chiapas, México*. Plaza y Valdéz / COCITECH / ECOSUR, México, D.F.
- Rosen, D.E. (1975) A vicariance model of Caribbean biogeography. *Systematic Zoology*, 24, 431–464.
- Rosen, D.E. (1979) Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. *Bulletin of the American Museum of Natural History*, 162, 269–375.
- Rosen, D.E. (1985) Geological hierarchies and biogeographic congruence in the Caribbean. *Annals of the Missouri Botanical Garden*, 72, 636–659.
- Royero, R. (1987) *Morfología de la Aleta Dorsal en los Bagres (Teleostei: Siluriformes), con Especial Referencia a las Familias Americanas*, Undergraduate thesis Universidad Central de Venezuela, Facultad de Ciencias, Escuela de Biología, Caracas, 232 pp.
- Savage, J.M. (1982) The enigma of the Central American herpetofauna: dispersals or vicariance? *Annals of the Missouri Botanical Garden*, 69, 464–547.
- Schaefer, S.A. (1987) Osteology of *Hypostomus plecostomus* (Linnaeus) with a phylogenetic analysis of the loricariid subfamilies (Pisces: Siluroidei). *Contributions in Science, Natural History Museum, Los Angeles County, California*, 394, 1–31.
- Schaefer, S.A. (1990) Anatomy and relationships of the scoloplacid catfishes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 142, 167–210.
- Shibatta, O.A. (1998) *Sistemática e Evolução da Família Pseudopimelodidae (Ostariophysi, Siluriformes), com a Revisão Taxonômica de Gênero Pseudopimelodus*, Ph.D. thesis Univ. Fed. São Carlos, São Paulo, Brazil, 357 pp.
- Stehli, F.G. & Webb, S.D. (1985) *The Great American Biotic Interchange*. Plenum Press, New York, New York, USA.
- Teugels, G.G. & Adrians, D. (2003) Taxonomy and phylogeny of Clariidae: an overview. *IN*: Arratia, G., Kapoor, B. G., Chardon, M. & Diogo, R. (Ed) *Catfishes*. Science Publishers, Inc., Enfield, NH USA and Plymouth, UK, 317–352.
- Wendt, T. (1998) Composición, afinidades florísticas y orígenes de la flora arbórea de dosel de los bosques tropicales húmedos de la vertiente mexicana del Atlántico. *IN*: Ramamoorthy, T. P., Bye, R. A., Lot, A. & Fa, J. (Ed) *Diversidad Biológica de México*. Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, 581–664.